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## GALLS AND INSECTS PRODUCING THEM.

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### PART III. LATERAL BUD GALLS.

In Part II of this series of papers I gave a discussion of apical bud galls. The lateral bud galls differ from the apical only in point of location; therefore, this (Part III) may be considered a continuation of Part II. There is, however, considerable difference in the galls dependent upon the order and genus to which the insect belongs and to the part of the plant which is attacked by the enemy. These differences may be summed up briefly as follows:

(1) Affection of the tip of the stem causing it to remain in its incipient condition and the leaves to remain aborted, instead of lengthening. This is well illustrated by the apical bud galls of *Cecidomyia solidaginis* Lw. on Solidago; *Cecidomyia salicis strobiloides* O. S. on Salix; and *Callirhytis clavula* Fitch on Quercus alba. (Part II, Figs. 31, 32, 33.) In these cases we have two orders of insects represented but producing similar galls: this, as previously explained, is no doubt due to the fact that the insects affect corresponding parts of the host plant.

(2) Affection of the tip of the bud causing it to remain short but to become large and globular. This is well illustrated by *Holcaspis globulus* Fitch (Fig. 34, a, b, c.) By collecting specimens of this gall in April or early part of May it is easy to demonstrate that the gall is in reality an enlargement of the stem part of the bud. The insect evidently deposits the egg in the apical part of the incipient stem. This causes the stem to enlarge, forming a globular body, but to remain so short as to form a sessile gall on the main stem. The bud scales are at first very prominent but gradually shrivel up and are lost, leaving a naked,

globular gall. At this late stage the only evidence that we have of its bud origin is its location at the node of the main stem. The transition from bud to gall occurs very early, before there is any differentiation of the parenchyma tissue ; examination of the structure of the gall fails to show any stem characters but does show the Cynipidous gall character described in Part I of this series.

(3) The third type of the bud gall is illustrated in *Andricus seminator* Harris (Figs. 35, a, b, and 36, a, b.) Ashmead* refers to this as a flower gall. It is not difficult to demonstate that this gall is a true, compound bud gall, but whether it is a flower or leaf gall is not so easily determined. The strongest evidence of its bud character is its location at the node of the stem and the presence of the leaf scales at its base. The writer gathered and dissected a large number of galls of various ages and is confident that this is a true compound bud gall. In Figure 35 a, we have a short twig with three buds, one of which was attacked by the insect ; the other two buds remained unaffected Around the base of the gall are four well-defined bud scales. In Figure 35 b, two buds were affected ; one of these has been removed showing the scar where it was attached and also exposing the back side of the compound gall formed from the other bud. A great many galls of various ages were dissected ; the younger ones showing the bud scales and the older ones showing the well-defined scars by which it was easy to trace the number of buds affected. Careful observations were made in hopes of finding a gall which would show whether this was a leaf or flower bud, but without success. However, from a careful microscropic examination of a number of galls I am inclined to consider it a leaf bud, in which each leaf becomes a single gall of the large cluster and in which the incipient stem remains short. The microscopic examination of the single galls (Fig. 36, a, b) shows that each gall contains at least one (and usually only one) fibro-vascular bundle which in most cases is very much atrophied and in some cases so much reduced as to be very indistinct. The writer considers the fibro-vascular bundle as the mid-rib of the modified leaf and the cottony part of the gall as the mesophyll part of the leaf. This gall does not show the four zones which are characteristic of the cynipodous galls as pronounced as other galls which we have examined, but this point will be discussed in a later paper.

(4) The fourth type of gall is illustrated by a cecidomyid gall (Fig 37) found upon Acer negundo in which the bases of the petioles of a number of leaves from the same bud are enlarged,

*Ashmead, Wm. H.: "On the Cynipidous Galls of Florida, with descriptions of new species and synopses of the described species of North America." Trans. Amer. Ent. Soc. Vol. XIV, pp. 125-128.

thus forming a bulb-like compound gall. On the inner surface of the base of each petiole is a cavity containing the larva. The stem remains short but the outer leaves are fully developed in most cases.

(5) *Pachypsylla celtidis-gemma* Riley (Fig. 38) is evidently a bud gall very similar to the preceding. Only advanced stages of this gall were collected, and therefore its development could not be observed. From the specimens collected it appeared that each scale and undeveloped bud formed a pocket for the insect, there being a single insect under each scale.

CONCLUSIONS.

Bud galls are subject to considerable variation due to the fact that they are produced by insects of different orders and that these insects attack different parts of the buds and different tissues in these parts. In all cases except the fourth the demands of the insect are so great as to cause a very pronounced change in the bud. In the fourth the modifications are not so pronounced as in the other four types.

## PART IV. STEM GALLS.

Stem galls, according to my definition, include only those galls which cause a swelling of the stem and with the larva placed in or near the center, thus affecting the stelar and fibro-vascular parts of the stem. This definition may not be as broad as it should be, but I hesitate to make it include other forms until I have had an opportunity to make a more careful examination of the questionable forms. The fact that such galls as H. globulus (Fig. 34, a, b, c), which is frequently mentioned as a stem gall, are in reality bud galls, leads me to be doubtful of the origin of galls which have similar locations. Many of the so-called stem galls may be in reality bud galls and this point can be determined only by a study of their development and structure.

Some galls occur on both leaves and stem, but in these cases the gall affects only the outer layers of the cells of very young twigs and these cells at this time resemble the leaf cells in both structure and functions. *Phylloxera carya-spinosa* Shimer (Part I, Fig. 19) and *Phylloxera caryae-caulis* Fitch (referred to in Part V) are good examples of leaf galls affecting stems.

The Lepidopterous galls are usually stem galls and may be either solid or hollow and are most common on Solidago. In studying such galls it is necessary to examine first a normal stem.

The stem of Solidago (Fig. 39) shows the ordinary dicotyledonous character. The epidermal cells (e p) are firm and rather hard. Just below these cells is the parenchyma zone (p a) of closely-fitted cells and few intercellular spaces. Below the parenchyma zone are the fibro-vascular bundles (p. v. b.), which

contain a large amount of woody, fibrous tissue. Inside the zone of fibro-vascular bundles and forming the axis of the stem, is the stelar (st) made up of large parenchyma cells.

In *Trypeta solidaginis* (Fig. 40) a solid globular gall on the stem of Solidago, we find the walls of the outer parenchymatous cells much thickened and numerous large intercellular spaces which are not characteristic of the unaffected stem (Fig. 39). The fibro-vascular bundles (f. v. b.) are spread out and flattened, the sclerenchyma tissue and tracheary tissue being reduced and the fibrous tissue increased in amount. The parenchyma tissue of the stelar (st) part of the gall is increased in amount and the size of the cells reduced. This tissue is undoubtedly very active and well supplied with nutrition for the larva. Throughout the tissue are tubes (tu) lined with cells smaller than the parenchyma cells, brown in color, and not affected by haematoxylin stain. These tubes are usually associated with small bundles of fibrous tissue and are probably important factors in the nutrition of the larva. They were not found in sections of normal stem of corresponding age.

In *Gelechia gallae-solidaginis* Fitch (Fig. 41) an elongated, hollow gall on Solidago, we find the parenchymatous tissue (pa) near the surface increased in amount, the cells larger and the walls thicker than in an unaffected stem, but no intercellular spaces such as are found in T. solidaginis. The fibro-vascular bundles (f. v. b.) undergo comparatively little change, becoming slightly flattened and thinner and with a reduction of the firmer fibrous tissue. The larva chamber (l. c.) of the gall is lined with a few layers of small parenchymatous cells (st) and is the stelar part of the stem. This parenchymatous tissue is udoubtedly used for food.

In *Cecidomyia rigidae* O. S. (Fig. 42) an elongated, hollow gall common on Salix discolor, usually near the tips of the twigs, we find considerable modification of the normal stem structure. From the examination of a number of specimens it is very clear that the enlargement of the stem is due to two factors: the formation of large intercellular spaces near the surface, similar to those in T. solidaginis (Fig. 40), and the formation of the larval chamber (l. c.) in the stelar part of the stem. The parenchymatous tissue lining the chamber is made up of cells very much smaller than those in an unaffected stem.

The Lepidopterous galls on the young stems of Acer negundo and Coleopterous galls on Rubus villosus were examined but no new points presented. I was unable to secure satisfactory specimens of stem galls of Cynipidae.

Although the study of stem galls was in many respects unsatisfactory, I feel justified in giving the following brief conclusions:

CONCLUSIONS.

1. Stem galls show less variations than any other group of galls, although they may be produced by insects from widely different orders. This is undoubtedly due to the fact that the various insects attack corresponding parts of the host plants. In proof of this fact, it will be noticed that all these insects deposit the egg within the tissues of the host plant and not on the surface.

2. The galls in general show an increase of parenchyma below the epidermis, either a thickening of cell walls or a development of intercellular spaces, a flattening of the fibro-vascular bundles, an increase of parenchyma tissue in stelar part of stem and a decrease in size of same.

## PART V. DEVELOPMENT OF GALLS.

A very large amount of material was collected for this paper and great difficulty was experienced in getting the extremely young stages because of the fact that young specimens were difficult to recognize and identify. The material was carefully killed in either Fleming's solution or chromo-acetic, passed through the alcohols, imbedded in paraffin, sectioned on a Zimmerman microtone and stained in haematoxylin.

The galls will be considered in the same order as in Part I of this series. A consideration of the leaf structure is unnecessary since that was considered in Part I.

### 1. GALLS OF ACARINA.

Young galls of *Phytoptus quadripes* (Fig. 43), *P. abnormis* (Fig. 44), and *P. acericola* (Fig. 45) were studied, and all show the same developmental characters. The leaf becomes slightly pitted on one side (usually the lower) and a corresponding elevation is formed on the upper surface. This gradually enlarges until the more or less spherical gall is produced. In P. abnormis the spherical gall soon assumed an elongated form. The characteristic cell structure of the leaf is lost and the cells become very irregular in shape. The elongated character of the cells just beneath the outer epidermis appears at a later period of the development. At first the inner surface of the gall is perfectly smooth, but very soon masses of cells are formed and project into the cavity (Figs. 43 and 45). At about the same time trichomes begin to develop from the inner epidermis (Fig. 44) and project into the cavity. These trichomes grow very rapidly and almost fill the entire cavity.

In the very young galls no fibro-vascular bundles are formed, but in the older galls small bundles of fibrous tissue are numerous.

The first effect of the insect attack is undoubtedly to cause an increase in the number of cells, which is an effort on the part of the plant to heal the wound produced by the repeated puncturing

of the cells by the parasite. Since the parasite continues its attack upon different cells and the plant makes the repeated effort to heal the wound, we have the very active production of cells. The parasite making its attack upon one side of the leaf, causes the unequal growth resulting in a cavity. The increase in size of the gall causes a different tension upon the inner and outer surfaces and results in the elongation of cells near the outer surface as described in Part I.

When the galls first appear they are single, but in a very short time others are formed just outside the first, thus forming a cluster.

In *Erineum anomalum* (Figs. 47, 48, a, b), occurring on leaves and petioles of walnut, we find a condition similar to that of the Phytoptus galls except that the parasite is on a free surface instead of in a partly closed cavity. I was able to secure a very complete series of this gall. The first indication of the gall on the petiole or rib of a leaf is the increase in the amount of parenchyma tissue between the epidermis and fibro-vascular bundles. The physiological character of this tissue is also changed to some degree, since the cells are not so easily stained with haematoxylin, have rather thick walls, and contain a considerable quantity of tannin. The epidermal cells now begin to form trichomes (Fig. 47). The parenchyma tissue and trichomes both increase in quantity, the walls of the cells become thinner (Fig. 48, a, b), and the deeper parenchyma tissue gradually loses its tannin, while the outer cells retain it in great quantities.

These galls always occur over a fibro-vascular bundle and are apparently closely associated with them. These bundles become modified to some extent.

The origin and development of these galls is the same as in the Phytoptus galls except that the parasite works upon the exposed surface instead of in a cavity. The fact that one produces a cavity lined with trichomes while the other produces a protuberance covered with trichomes, is probably due to the fact that the latter is so closely associated with the fibro-vascular bundle which prevents the curvature but causes the rapidly-formed cells to swell outward into a protuberance.

### 2. GALLS OF THE APHIDIDAE.

In the Aphididae galls we have a condition very similar to that just described for the Acarina galls except that the shape of the galls are far more definite and they show a higher degree of development. Trichomes are not so numerous and masses of cells projecting into the larval chamber as described for Phytoptus galls are very rare. In the youngest galls the cell structure of the leaf is modified, resulting in the formation of a large number of small, irregular cells, the same as in the Acarina galls. As the

galls grow older the cells near the outer epidermis become elongated as in the Phytoptus galls.

In *Pemphigus ulmifusus* (Walsh) Oestland (Fig. 49, a, b) on U. Americana, we have the gall originating first as a fold in the leaf which becomes developed into a conical structure. The structure of the gall shows that the characteristic structure of the leaf is at first modified into a large number of small, irregular-shaped cells (Fig. 49, b). The tendency for the cells near the outer surface to elongate parallel to the surface begins with the further development of the gall. In the very young galls the tannin is in very small quantities, but increases as the gall grows older.

In *Colopha ulmicola* Fitch (Fig. 50, a, b) we have a condition almost identical with P. ulmi-fusus. The gall first appears as a slight fold in the leaf and later develops into the characteristic cockscomb gall. The cell structure is the same as in P. ulmi-fusus.

In *Phylloxera carya-fallax* Riley (Figs. 51, 52) on H. ovata, I secured the youngest galls possible to detect and identify. These galls showed a slight projection from both surfaces of the leaf, but at first the gall was not so conical as at a later period of its development. However, the youngest galls showed the characteristic structure described in Part I of this series. The first effect of the parasite attack appears to be the formation of a large number of irregular cells. The arrangement of these cells is the same in the young gall as in the more mature, but the fibro-vascular bundles of the older specimens were not observed in the young galls.

I was not so successful in securing young specimens of P. c.-globuli Walsh (Fig. 53), but, so far as I was able to observe, the line of development coincided with P. c.-fallax. However, the upper wall of the gall is at first very thin and grows in thickness as the gall approaches maturity.

*Phylloxera carya-caulis* Fitch of Hickory ovata was studied very carefully from a very complete series of specimens. The material, especially the younger galls, did not cut well, and so was not satisfactory for drawings. However, the development and structure were of the typical Phylloxera type corresponding very closely with that just described for P. c.-fallax. The only marked peculiarity was the close association with fibro-vascular bundles, the galls always occurring on very young green twigs, on mid-rib or on prominent veins of the leaf.

*Pemphigus populi-transversus* Riley (Figs. 55, a, b, and 56, a, b) and *P. p.-caulis* Fitch (Figs. 57, a, b, c, and 58, a, b, c) of the Populus are galls growing on the petiole; the former at some point between the blade and stem, the latter at the base of the leaf. In both cases the attack is made from the outside, the same as in other Aphididae galls and in the Acarina galls. A careful

study of an excellent series of both galls shows a cell structure and development very similar to other Aphididae galls; i. e., a large number of small, irregular cells. In P. p.-transversus (Fig. 55, a, b) the gall originates as a swelling on the petiole and within this swelling is a large cavity opening to the outside through a slit. In the P. p.-caulis the same condition is true but the attack of the insect causes a one-sided growth, resulting in the petiole being twisted at right angles to the blade (Figs. 57, a, b, c, and 58, a, b, c).

A careful examination of the cell structure of P. p.-transversus (Fig. 56, a, b) and a comparison with the unaffected petiole (Fig. 54, a, b) indicated a very rapid growth, resulting in the very large number of small, irregular cells. The character of the young and of the mature gall was practically the same, and not different, as in the more highly developed galls of other orders. The fibro-vascular bundles were very slightly affected.

P. p.-caulis showed the same cell structure and development, and, judging from these points alone, one would be unable to separate these two galls.

### 3. GALLS OF PSYLLIDAE.

In *Pachypsylla celtidis-mamma* Riley (Figs. 59 and 60, a, b, c) of the Celtis occidentalis the youngest galls did not show a cavity, but showed a modification of the leaf by which there is formed a large number of small, irregular cells which can be readily separated into two zones; the upper made up of small, and the lower of somewhat larger cells (Fig. 59). I was unable to secure specimens intermediate between this stage and a later stage, showing the true form of the gall (Fig. 60, a, b, c) The youngest galls, showing the true form, exhibited four well-defined zones: (1) epidermis, (2) zone of large, irregular-shaped cells, (3) zone of elongated cells, (4) zone of irregular-shaped cells next to the larval cavity. Adjacent to zone (3), but derived from zones (2) and (4), are cells which even in very young galls show schlerenchyma characteristics. As the gall approaches maturity this tissue increases until in the mature gall it may be found in great abundance. This gall is undoubtedly the most highly developed of any of the Hemiptera galls which I have studied.

### 4. GALLS OF CECIDOMYIA

Although I have a large number of Cecidomyia leaf galls, I have succeeded in getting a series of only two species. Since the Cecidomyia show by far the greatest variation in structural characters and the smallest number of typical group characters, two species are not sufficient to draw a very definite conclusion.

In *Cecidomyia gleditsiae* O. S. (Fig. 61, a, b) the two halves of the leaflet never have an opportunity to unfold, but there is a

growth of cells allowing the leaflet to enlarge and form the larval chamber between the two halves. The cells are at first normal, but gradually lengthen in an axis at right angles to the mid-rib. This can be readily observed by comparing the section of the very young gall (Fig. 61, a, b) with the section of the mature gall (Part I, Fig. 22).

In *Cecidomyia verrucola* O. S. (Figs. 62 and 63) the youngest showed a condition in which the mesophyll part of the leaf was reduced or entirely removed by the larva. The upper epidermis and palisade cells, the lower epidermis and cells next to it, form the upper and lower walls of the larval chamber while the intermediate mesophyll is removed. The inner layers of cells, i. e., the cells next to the larval chamber, now grow and divide very rapidly, gradually filling almost the entire cavity and reducing the size of the chamber (Part I, Fig. 24). At the same time the gall is increasing rapidly in size.

### 5. GALLS OF THE CYNIPIDAE.

Although a large amount of material was collected, only three species were sufficiently complete to enable a satisfactory study. However, several mature galls of species not described in Part I of this series were examined, and all agreed with the statements made concerning the general structural character of this group of galls.

*Callirhytis papillatus* O. S. (Fig. 64) was especially difficult to collect because of its very small size and close resemblance in external appearance to other small Cynipidous galls. Examination of young Cynipidous forms, which I am reasonably certain belong to this species, show all the zones in contact (Fig. 64). As the gall develops the protective zones and parenchyma zones separate but remain connected by elongated parenchymatous cells (Part I, Fig. 30).

*Dryophanta palustria* O. S. (Fig. 65, a, b) appears as the leaves unfold from the bud. The youngest galls collected were not over two millimeters in diameter but showed the four zones well developed, with the second and third zones in contact, thus verifying the views expressed in Part I. The cells of the innermost, or nutritive, zone were large and very granular. Evidently this zone was almost completely reduced by the larva in the specimen from which Fig. 29 of Part I was drawn. In the next, or protective, zone the cell walls were very thick. In the parenchyma zone the innermost cells were small and numerous and the walls were thin, and in both cases the long axis of the cells were at right angles to the surface of the gall. As the gall grows older the intercellular spaces may become prominent among the cells of the parenchyma zone (Fig. 65, b). Careful examination of a large number of specimens gave conclusive proof that the separation occurs

between the protective and parenchyma zones, thus leaving the two inner zones as a small sphere rolling free within the larger sphere which is formed by the two outer zones.

In *Diastrophus siminis* Basset (Figs. 66, a, b; 67; 68, a, b, c, d; 69) we have a Cynipidous gall occurring on Nepeta glechoma. I secured a very complete series of this gall and made a very careful study of its development. In the youngest gall (Fig. 66, a, b) we have the cell character of the leaf transformed into a mass of small, irregular cells which can be readily divided into two zones, the outer of which has the larger cells. At this time the cells are very compact, but as the gall grows older intercellular spaces are developed, the entire structure becomes loose and spongy and the cells become larger.

As the galls grow older a well-defined zone of flattened cells is developed in the parenchyma near the epidermis, and fibro-vascular bundles (f. v. b.) are developed at right angles to the surface (Fig. 67). Up to this time the cells are small, irregular and compact. The epidermis (ep) and parenchyma (pa) zones are well defined, but the distinctiion between protective and nutritive zones cannot be made.

As the gall grows older a cleavage plane is formed in the parenchyma just inside the zone of flattened cells (Fig. 68, a). A careful examination of the parts thus cut off and surrounding the larval chamber (l. c.) shows two well-defined zones which correspond to the nutritive and protective zones described in Part I. At this time there is no marked difference in the amount of food supply of the two zones. In the outer part formed by this cleavage plane we have the parenchyma (pa) and epidermal (ep) zones (Fig. 68, c). Connecting the parenchyma and protective zones we find fibro-vascular bundles (f. v. b.) surrounded by parenchyma cells (Fig. 68, d). The character of these connecting strands is very similar to that described for H. centricola (Part I, Fig. 27) and A. inanis (Part I, Fig. 28), but contains more parenchyma tissue than either. However, the parenchyma cells are not so elongated as in C. papillatus (Part I, Fig. 30). As the gall grows older the cells of the protective zone become clear and the cell walls of the nutritive zone gradually thicken (Fig. 69), many undergoing complete degeneration, while others assume the character of the sclerenchyma.

## CONCLUSIONS.

1. All conclusions given in Part I are emphasized by the study of the development of the galls.

2. In the formation of all leaf galls except the Cecidomyia galls, the normal cell structure of the leaf is first modified by the formation of a large number of small, compact, irregular-shaped cells. In the galls of Acarina and Aphididae this is followed by

a development of trichomes, especially the former. In all galls the mesophyll is subject to the greatest modification. Many small fibro-vascular bundles are formed in this modified mesophyll.

3. The Acarin may be considered the lowest group of galls, the Aphidid the next higher, the Cecidomyia galls the next higher, and the Cynipidous galls the highest. However, many of the Cecidomyia galls are lower than the Aphidid galls.

4. The galls of Acarina and Aphididae show the greatest resemblance. In these cases the method of attack is very similar and is first directed against the epidermal or adjacent layer of cells.

5. In some of the Cecidomyia galls (e. g. C. verrucola) the larva appears to make its entrance into the mesophyll before there is any pronounced modification of the cell structure. However, the Cecidomyia galls are too varied and the study too incomplete to make a positive conclusion.

6. Both Adler and Fockeu consider that after the first stages of formation, the gall becomes an independent organism growing upon the host plant. This is probably true in the highly developed galls of Aphididae, Cecidomyia and Cynipidae, but the writer is very doubtful if this is true of the less complex galls of Acarina, Aphididae and Cecidomyia.

This work was pursued during the year 1902–03, in the Biological Laboratory of DePauw University, but was under the supervision of Professor Herbert Osborn, of the Ohio State University, to whom I am indebted for many valuable suggestions. I am also indebted to two of my former students, Miss S. Emma Hickman and Miss Margaretta S. Nutt, for aid in preparing slides and making drawings. Drawings made by these two ladies are marked with their initials. I also wish to express my thanks to my many friends who have called my attention to, or have collected material for, these investigations.

## LITERATURE.

New literature will not be cited at this time, but a more complete list will be given in connection with later papers upon this subject.

## EXPLANATION OF PLATES.

In making the drawings a Bausch & Lomb microscope, with No. 2 ocular and 1/6 objective, and a B. & L. camera lucida were used. The drawings are, therefore, larger than those used in Parts I and II, and the reduction not so great. The diagrams are not made upon a definite scale. Drawings 34, a, b, c; 35, a, b; 37, 38, 55, a, b; 57, a, b, c, and 58, a, b, c, were made from nature, and are very little smaller than the original. The numbering of the drawings is continuous with Parts I and II.

ABBREVIATIONS.

ep.—epidermal zone.
pa —parenchyma zone.
pr.—protective zone.
nu.—nutritive zone.
f. v. b.—fibro-vascular bundles.

34, a. Bud of Hicoria ovata.
34. b, c. Holcaspis globulus on H. ovata.
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68, c. " " Epidermal and parenchyma zones.
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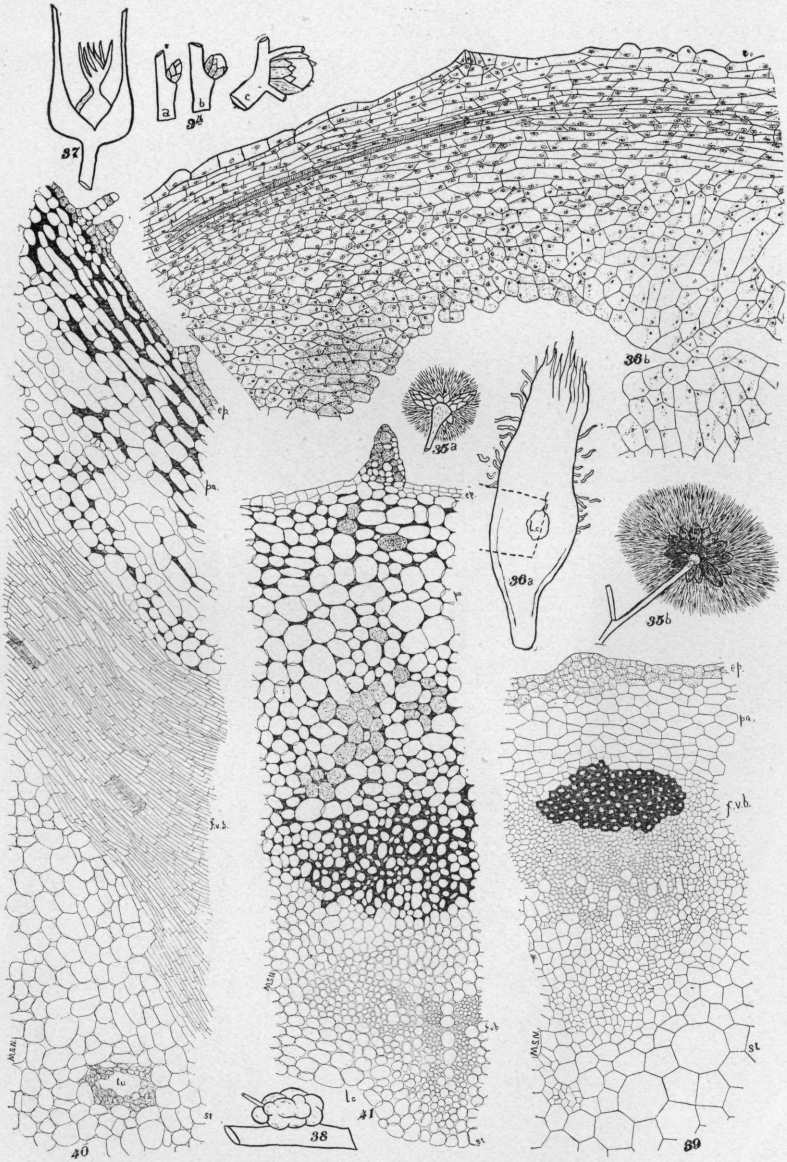
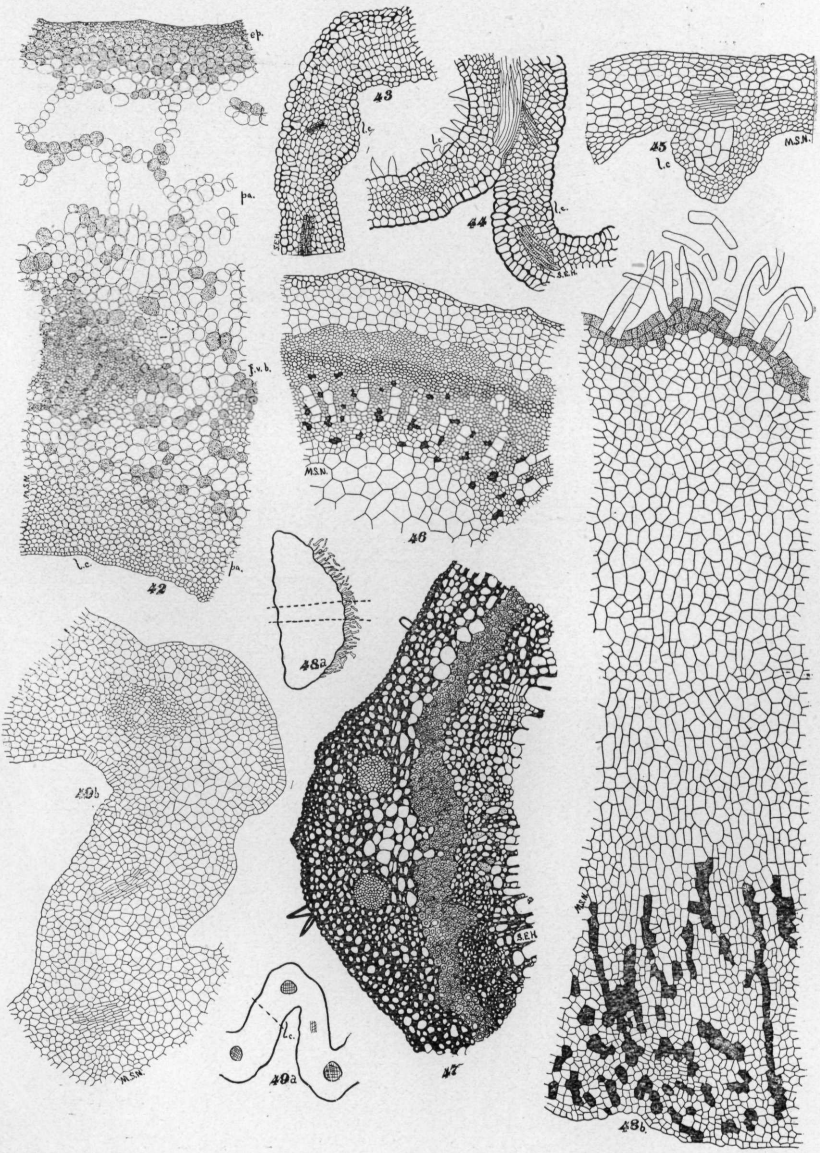
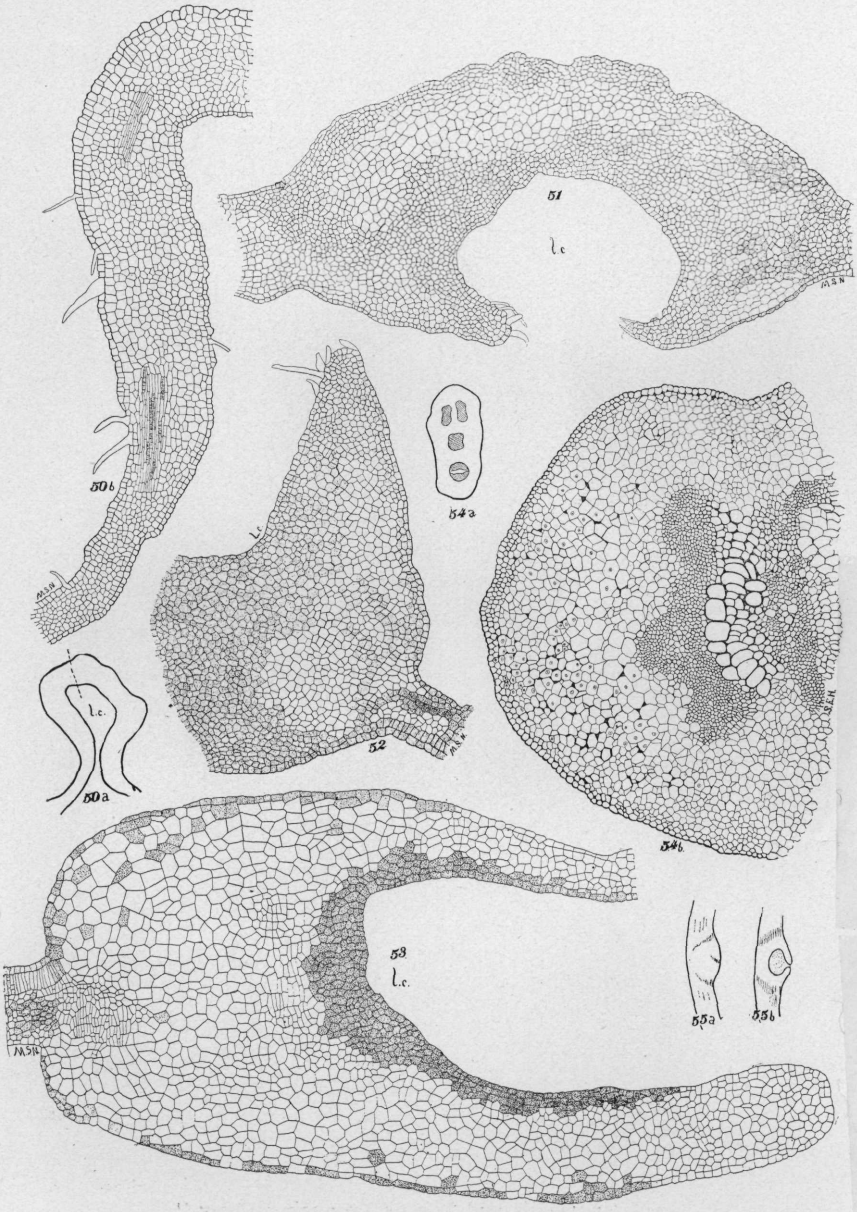



COOK on "Galls and Insects Producing Them."

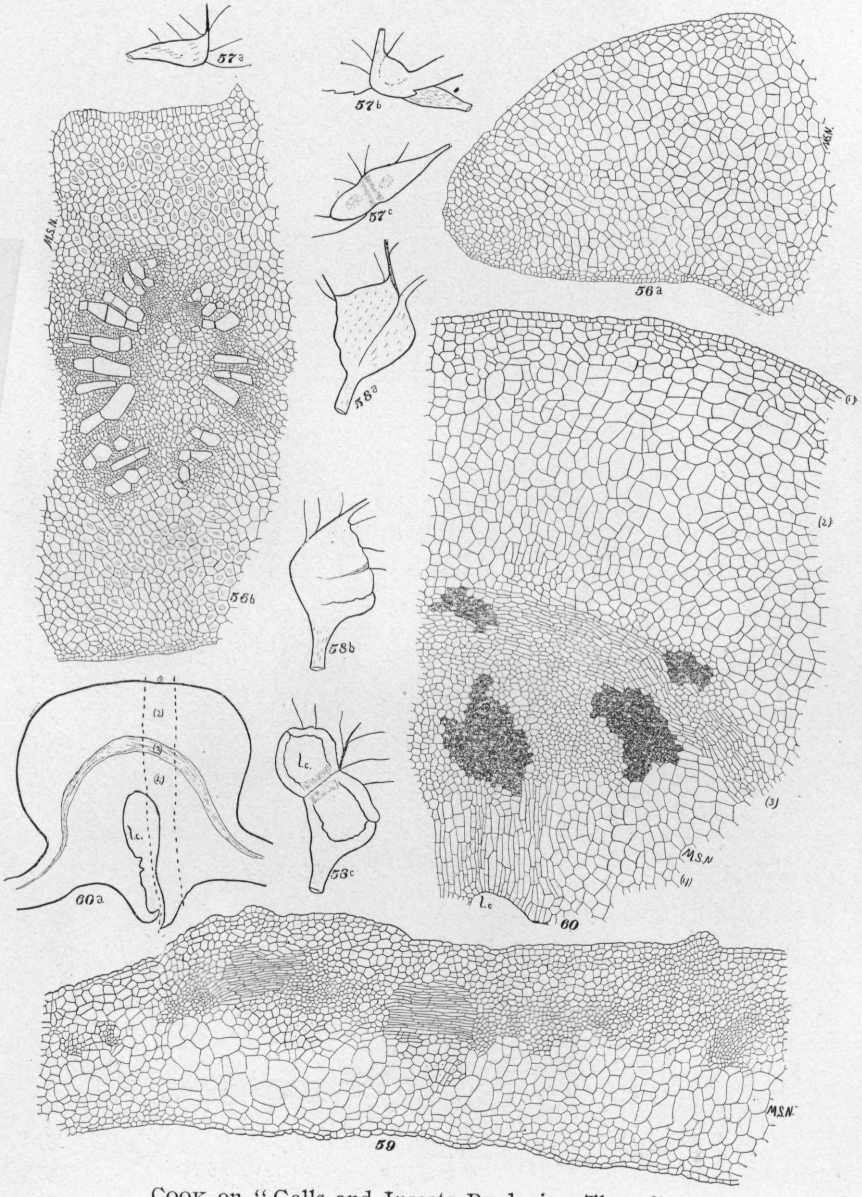
OHIO NATURALIST. *Plate 14.*



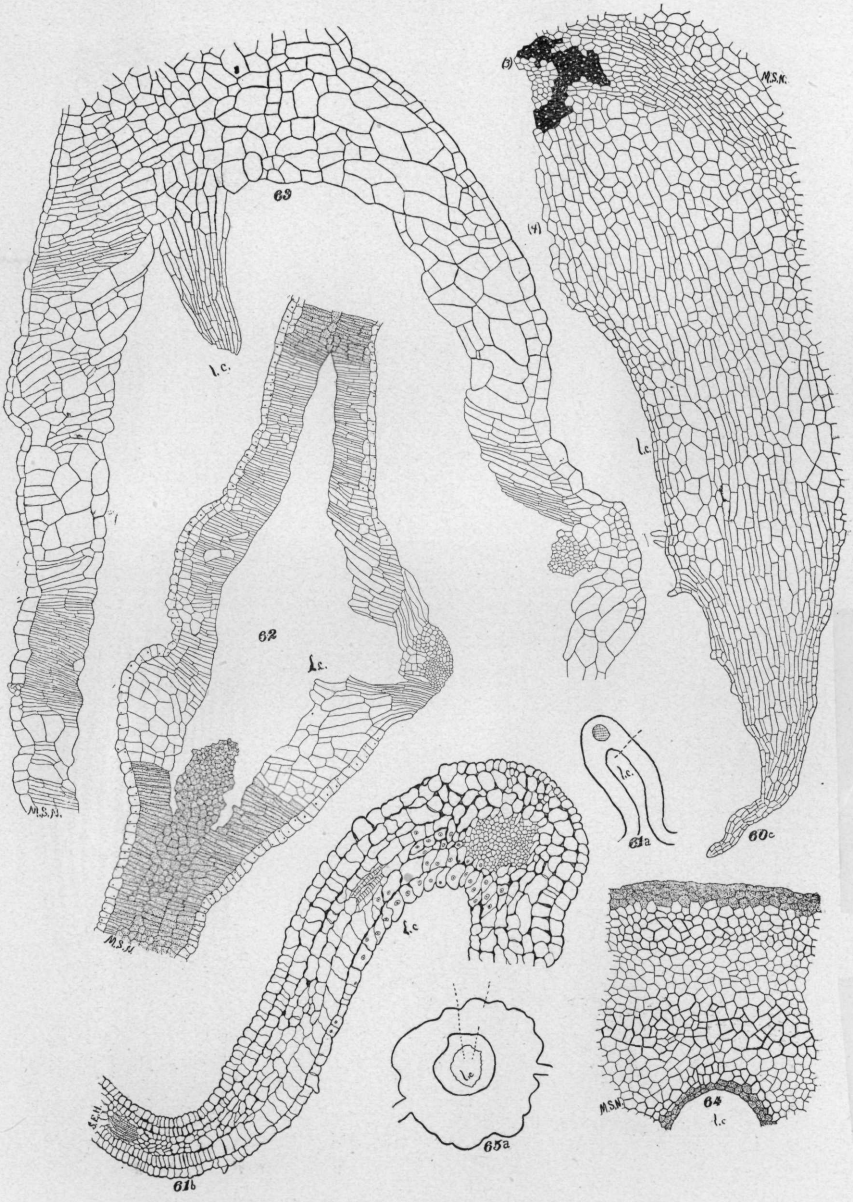

COOK on "Galls and Insects Producing Them."




COOK on "Galls and Insects Producing Them."

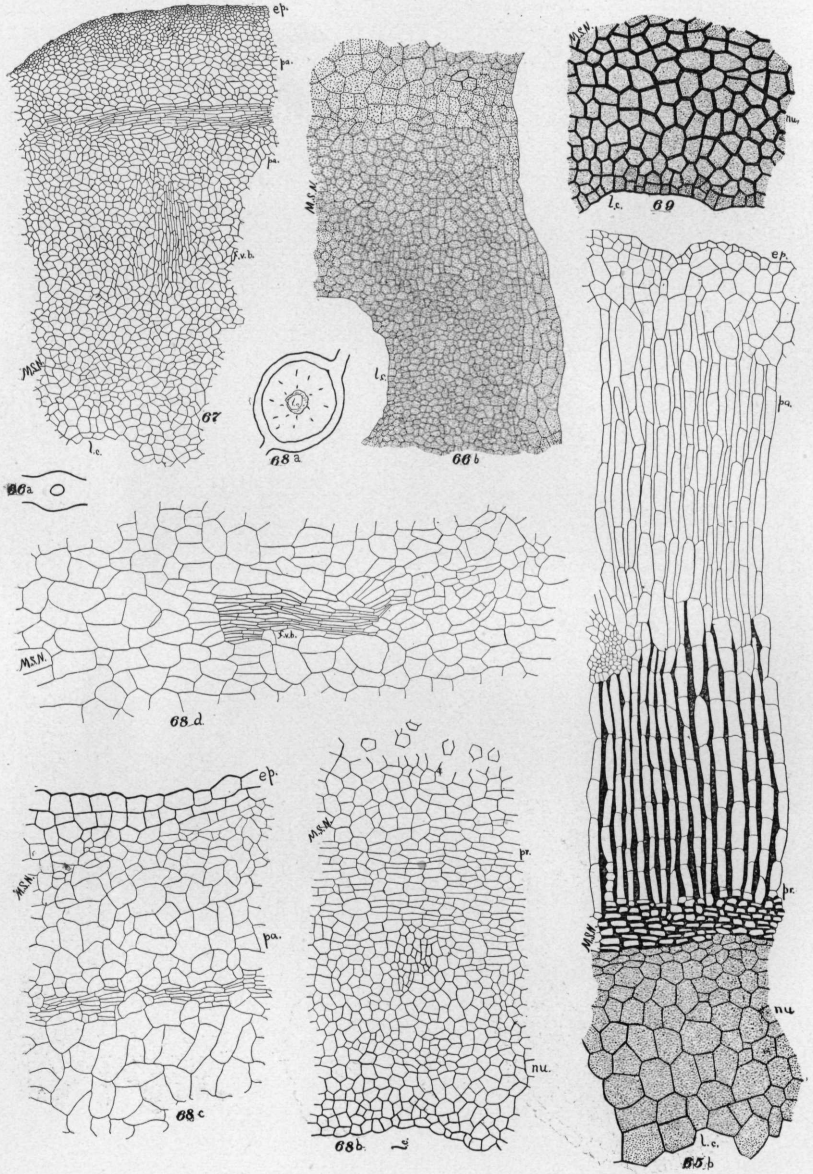



COOK on "Galls and Insects Producing Them."




COOK on "Galls and Insects Producing Them."

OHIO NATURALIST. *Plate 18.*




COOK on "Galls and Insects Producing Them."